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STUDIES ON TETRAPHYLLIDEAN AND TETRARHYNCHIDEAN METACESTODES FROM SQUIDS TAKEN ON THE NEW ENGLAND COAST [1]

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Early investigators, Verrill, Baird, Leidy, and others, studied the marine fauna of the Atlantic coast of North America. They reported developmental stages of tapeworms in various invertebrates and in fishes. Morphological agreement of plerocercoids from the several host-species presaged taxonomic relationship but posed an enigma: the presence of similar larvae in such diverse host-species. No information on life-histories of marine cestodes was available, and determination of life-cycles under experimentally-controlled conditions was far in the future. Professor Verrill of Yale University had published his monograph on the vertebrate animals of Vineyard Sound and in 1881 directed Edwin Linton, a young graduate student, in the study of helminthic parasites of fishes. It was the first systematic investigation of helminthic parasites in America. The study was continued for the next forty years, chiefly in the laboratories of the U.S. Fish Commission at Woods Hole, Massachusetts; Beaufort, North Carolina; Flatts, Bermuda; and Tortugas, Florida.

Now, a century later, information on these cestodes is still meager, and no life-history has been experimentally demonstrated. But it is clear that the worms have three larval stages and three successive hosts in the life-cycle; that they belong to the two orders, Tetraphyllidea and Tetrarhynchidea, and that they become mature in the spiral valve of selachian fishes. The collecting department of the Marine Biological Laboratory provides large numbers of squid, *Loligo pealcii*, for experimental work on neurophysiological problems and this material afforded the opportunity to study the cestode larvae harbored by them. The morphology and taxonomic relations of the plerocercoids are presented in this report.

Larval cestodes encysted in marine fishes have been known since O. F. Mueller (1787) erected a genus, *Scolex*, for three unnamed species. According to Stiles and Hassall (1912), *Scolex* was not proposed as a larval genus and *Scolex pleuronectis* Mueller, 1788 was accepted as type. *Scolex lophi* Gmelin, 1790; *Scolex cyclopteri* Fabricius, 1794; *Scolex marinus* Fabricius, 1794; and *Scolex pleuronectis platessa* Viborg, 1795 were named before 1800. All were found in fishes. The doubtful validity of these variable and inadequately described species led Rudolphi to suspect that all were members of a single species, which he (1819) designated as *Scolex polymorphus* Rudolphi, 1819. Later observations disclosed that these worms are juvenile forms of strobilate cestodes and that the name, *Scolex*, referred to a group of larval stages and corresponded to the names, *Redia* and *Cercaria*, that were proposed initially as generic designations. These parasites are often described as larvae, but actually they are juvenile stages of tapeworms that com-

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plete their development and become sexually mature in the digestive tracts of elasmobranch fishes, sharks and rays. For these post-larval stages, Wardle and McLeod (1952) proposed the term, metacestode, to conform with the designation, metacercaria, for the corresponding stage in the life-cycles of digenetic trematodes. Metacestodes have been reported from various marine invertebrates as well as fishes, and it appears that fishes acquire the parasites by ingesting invertebrates. In a series of papers, Dollfus (1923, 1924, 1929, 1931, 1964, 1967, 1974) listed the cestodes of the plankton and the marine invertebrates. No complete life-cycle has been proved experimentally, but the pattern of development has been constructed from isolated observations on many species. Observations on development of certain species have made it possible to assign them tentatively to families in the orders Tetraphyllidea and Tetrarhynchidea.

The taxonomy and nomenclature of these cestodes is controversial. The name Tetraphyllidea was proposed by Carus (1863) to latinize the names, Tétraphyllidés van Beneden, 1849 and Tétraphyllés van Beneden, 1850, for the cestodes in which the scolex bears leaflike or earlike outgrowths. The cestodes in which the scolex bears armed, protrusible and retractile tentacles, also called proboscides, were listed as Tétrarhynques by Blainville (1828). The name Tétrarhynchidéa was proposed to replace Tétrarhynchidés Gervais and van Beneden, 1859 and the name was validated by Claus (1891) according to Olsson (1893). For this second group of cestodes, Diesing (1863) proposed the name Trypanorhyncha, and it has been widely adopted. Braun (1900) in *Bronn's Klassen und Ordnungen,* adopted the name Trypanorhyncha, while Fuhrmann (1930) in the *Kükenthal und Krumbach, Handbuch der Zoologie*, recognized the order Tetrarhynchidea. In the *Faune de France*, Joyeux and Baer (1936) accepted the order Tetrarhynchidea Olsson, 1893 and the same authors (1961) in the *Traité de Zoologie* attributed the order to Claus, after Olsson, with no date. There was no mention of the name Trypanorhyncha Diesing, 1863. Dollfus (1942) adopted "l'ordre des Tétrarhynques (Trypanorhyncha Diesing, 1863)" while Wardle and McLeod (1952) and Yamaguti (1959) recognized the order Trypanorhyncha Diesing, 1863, with no mention of Tétrarhynchidea. Since the group is based on the several larval forms described by Redi (1684) and included in the genus *Tetrarhynchus* Rudolphi, 1809, the name Tetrarhynchidea appears more appropriate. *The Rules of Zoological Nomenclature* do not pertain to suprafamilial names, and each author may decide which names to accept. In the proceedings of a symposium held under the auspices of the American Association for the Advancement of Science on systematics of cestodes, Marietta Voge (1969) recognized six orders, all with the ending, *idea*, including the Tetrarhynchidea.

The helminthic parasites of marine fishes of the Atlantic coast of North America were studied by Edwin Linton for a period of more than fifty years. He (1897a) described and figured tetraphyllidean, and tetrarhynchidean larvae from fishes and squids. Some of the material he had collected at Woods Hole, Massachusetts, and the rest consisted of a collection from the U.S. National Museum. Many of the figures are deficient and meaningless, whereas others may be identified with considerable assurance. On Plate II, figures 1 to 9 depict specimens from *Illex illecebrosus* that were designated *Phyllobothrium loliginis* (Leidy, 1887) Linton, 1897. Other metacestodes from the same host-species, shown in figures 10 and 11, can be

identified as *Dinobothrium septaria* (van Beneden, 1889) Braun, 1900. Figures 12 to 16, listed as *Rhynchobothrium* larvae from different fishes, suggest *Lacistorhynchus tenue* (van Beneden, 1858) Yamaguti, 1959. Figures 10 and 11, on Plate III and figures 3 to 8 on Plate IV are almost certainly of *L. tenue*. Indeed, Linton assigned the specimens to *Rhynchobothrium heterospine Linton*, 1890, now recognized as a synonym of *L. tenue*. Figures 9 to 12 on Plate IV were listed as *Rhynchobothrium imparispine* Linton, 1890, probably a synonym of *Grillotia erinaceus* (van Beneden, 1858) Yamaguti 1959, a species closely related to *L. tenue*, whose life-cycle was studied by Ruszkowski (1934). Figure 13 and 14 on Plate V were described as *Rhynchobothrium speciosum* new species; it was named type of a new genus, *Callotetrarhynchus*, by Pintner, (1931) and suppressed by Yamaguti (1959) as a synonym of *Tetrarhynchus gracilis* Rudolphi, 1819. Figures 1 to 5 on Plate VI were made from a single encysted specimen, designated *Otobothrium dipsacum* n. sp. The genus *Otobothrium* had been erected by Linton (1890) with *Otobothrium crenacolle* n. sp., a larva from various marine fishes, as type species. Dollfus (1942) included *O. dipsacum* in a new subgenus, *Pseudotobothrium*, which differs from *Otobothrium* in the length of the tentacular bulbs and the number of rows of large and small hooks on the tentacles. Yamaguti (1959) suppressed *Otobothrium insigne* Linton, 1905, as a synonym of *O. dipsacum*.

The biology and bionomics of the tetraphyllidean and tetrarhynchidean cestodes are known from fragmentary observations and from results of experimental studies on early larval stages. The adult stages of these cestodes live in the spiral valve of elasmobranch fishes, and eggs of the parasites fall with the feces to the bottom of the sea. There they become embryonated; the zygote develops to form an oncosphere, a hexacanth larva. The eggs of tetraphyllidean species are anoperculate, and the larvae emerge only in the intestine of an appropriate host, typically a copepod. The eggs of tetrarhynchidean species may be operculate; the oncosphere is enclosed in a ciliated covering, and the larva is known as a coracidium. The opercula open and the coracidia emerge. In both groups of tapeworms, the eggs or swimming coracidia are eaten by copepods. The oncospheres migrate from the intestine to the body-cavity of the copepod. There they undergo metamorphosis and transform into procercoids, mobile larvae with tail-like cercomeres in which the larval hooklets are extruded. As noted by Freeman (1973), the change from oncosphere to procercoid is a true metamorphosis, but later developmental stages do not involve a metamorphosis. In both tetraphyllidean and tetrarhynchidean cestodes, when the copepod is eaten and the procercoid is introduced into a second intermediate host, it drops the cercomere and again migrates from the intestine. The second intermediate host may be another invertebrate or a small fish. In it the procercoid develops into a plerocercoid; it may remain in the body cavity but typically the plerocercoid bores into the tissues and becomes encapsulated. If the second intermediate host is eaten by an unsuitable host, the plerocercoid again bores into the body-cavity and a plerocercoid may pass from one intermediate host to another and be re-encysted. Joyeux and Baer (1961, p. 451) distinguished between "hôtes obligatoire" and "hôtes d'attente" or paratenic. The first intermediate host is probably an obligatory species; the second and later hosts may be paratenic. The worms become sexually mature only in the intestine of elasmobranch fishes, sharks and rays.

Pintner (1913) proposed descriptive terms for regions of the metacestodes, and Dollfus (1942) adopted the terminology which has become widely accepted. In tetraphyllidean plerocercoids, the anterior region, *pars antica,* develops into the mature cestode, while the *pars postica* is a bladder-like region that is discarded later. The *pars antica* comprises the *pars bothridialis*, which bears the bothridia, an apical sucker, and a central stalk or peduncle; this portion becomes the scolex and is followed by a *pars proliferus*, the *Anlage* of the strobila. The bothridial region may be invaginated (Fig. 9) by retraction of the retractor muscle which originates in the wall of the *pars postica.* The invaginable region is known as the *pars vaginalis.* In the tetrarhynchid plerocercoid, there is a *pars bothridialis* but no apical sucker; and the stalk is long and contains the tentacles and the bulbs that operate them. The region containing the bulbs is known as the *pars bulbalis,* and its location has taxonomic significance. The *pars postica* is termed the blastocyst, and the *pars antica* may be retracted into it (Fig. 15). A tetrarhynchid that has lost its blastocyst is not comparable to a tetraphyllid plerocercoid and was termed a plerocercus by Dollfus (1942).

Early developmental stages, from the formation of the egg to the formation of the oncosphere, were traced in three tetraphyllidean species: *Acanthobothrium coronatum* Rudolphi, 1819; *A. filicolle* Zschokke, 1888; and *A. zschokkei* Baer, 1948 by Euzet and Mokhtar-Maamouri (1975) and of *Phyllobothrium gracile* by the same authors (1976). The most significant studies on the life-cycle of tetraphyllid cestodes were conducted by Euzet (1959). Eggs of *Phyllobothrium lactuca* van Beneden, 1850, from *Mustelus canis* were isolated in small bowls of aerated sea water. In seven days, at a temperature of 13 to 14 degrees, they contained oncospheres, but movement was feeble. Ten days after isolation, 98% of the eggs contained active larvae and they were placed in a bowl with freshly caught copepods. Eggs and free oncospheres were observed in the intestines of the copepods, and after five days oncospheres were present in the body-cavities of *Acartia clausi* and *Acartia discaudata.* Specimens of *A. discaudata*, examined 16 and 18 days after exposure, contained hexacanth larvae and procercoids of various sizes, some of which measured 200 to 400 μ long. Euzet declared, p. 227, "Cette expérience établit pour la première fois l'existence, pour les Tétraphyllidés marins, d'une larve procercoide chez les Copépodes." He concluded, p. 247, "D'aprés mes observations, les Cestodes peuvent se diviser en deux grands groupes. D'une part, ceux qui possédent une coracidie nageante (*Pseudophyllidea* et *Trypanorhyncha*), et d'autre part, ceux qui n'en ont pas et dont l'embryon hexacanthe sort de l'oeuf dans l'hôte secondaire ou définitif."

The post-embryonic development of various tetrarhynchidean species was studied by Pintner (1893, 1903), Ruszkowski (1932, 1934) and Dollfus (1942). Ruszkowski reported on the life-cycle of *Grillotia erinaceus* (van Beneden, 1858) Guiart, 1927, a parasite of *Raja oxyrhynchus.* The eggs were operculate and after an incubation period of 9 to 10 days, swimming coracidia emerged. They were eaten by copepods and the oncospheres were found in the hemocoel of the crustaceans. The oncospheres transformed and developed into procercoids with cercomeres which contained the larval hooklets. Ruszkowski described later stages from fishes to which the copepods were fed, but apparently did not complete the life-cycle experimentally. Dollfus (1942) reviewed the account of Ruszkowski and described the

formation and biology of the plerocercus of *Lacistorhynchus tenue,* using specimens found encysted in the pyloric caeca of *Scomber scomber.* His figure 241 depicts successive stages (a to g) and his Figure g is strikingly similar to Figure 15 of the present study. Dollfus (1942, p. 61) reported, "L'on peut admettre, par analogie avec ce qui a lieu pour les Pseudophyllides d'eau douce, que, lorsque le Copépode (ou peut être un autre invertébré planctonique) porteur du procercoide est ingéré par le deuxième hôte, le procercoide traverse, en abandonnant son cercomère, la paroi du tube digestif de ce deuxième hôte et passe dans la cavité générale. La partie antérieure du procercoide, celle que j'appelle le protéromère, devient plerocercus. Cela n'a pas encore été observé et l'on n'a pas non plus suivi un même individu dans toute la suite du dévelopment postembryonnaire, mais l'on a pu obtenir, pour quelques espèces, la série continue des états successifs par lesquels passe la larve (dans son deuxième hôte) pour arriver à l'état de plerocercus complètement formé avec scolex retiré dans le blastocyste. A l'état le plus jeune observé, le plerocercus en voie de formation apparait comme un massif plus ou moins ovalaire de parenchyme, limité par une cuticle; à un pôle, le parenchyme est plus condensé, avec pullulement de noyaux, c'est le pôle antérieur; au pôle opposé, il y a un pore excréteur auquel aboutit une paire de gros canaux excréteurs. Dans le parenchyme, il y a des ampoules excrétrices à flamme vibratile et des glandes unicellulaires. Il est vraisemblable que, dans ce premier état, le plerocercus est à peine avancé que peut l'être le protéromere du procercoide."

In an abstract, Riser (1951) reported experiments on the life-cycle of *Lacistorhynchus tenue,* and later (1956) he gave a more detailed account. Proglottids from the spiral valve of *Triakis semifasciata* yielded eggs, and coracidia emerged after four to five days of incubation. Oncospheres removed from coracidia were active, moving with hooks opposite the advancing end. Attempts to infect planktonic copepods were successful, but the copepods lived only two or three days. So recourse was taken to splash-pool copepods, *Tigriopus fulvus,* which were easy to rear under laboratory conditions. These copepods became infected, but the exoskeletons were so hard that the procercoids were not liberated in the digestive tracts of the fishes to which they were fed. The copepods were recovered from the feces of the fishes with the procercoids intact. Riser stated that all his material was sent to Dr. R. P. Dollfus for further study.

An interesting experiment was reported by Young (1954). Plerocercoids, identified as *Lacistorhynchus tenue,* were common in the surf-perch, *Cymatogaster aggregata* in San Diego Bay, California. A large, gravid female leopard shark, *Triakis semifasciata,* was autopsied and five unborn young were provided by Dr. Carl L. Hubbs of the Scripps Institution, La Jolla, California. Three young sharks were fed tetrarhynchid larvae from 30 May to 9 July and two were held as controls. One experimental fish was killed on June 4 and contained an immature tetrarhynch. The others were sacrificed July 16. The controls were negative; one experimental fish "contained a few, the other many tetrarhynchs." Whether or not the worms were mature was not stated.

Materials and Methods

The squids, *Illex illecebrosus* (Lesueur, 1821) Steenstrup, 1880 (syn. *Ommastrephes illecebrosa*) and *Loligo pealeii* Lesueur, 1821, in New England coastal

waters, harbor plerocercoids of tetraphyllidean and tetrarhynchidean cestodes. Squires (1957) reported that specimens of *Illex illecebrosus* from the Newfoundland fishing area were parasitized by larval tapeworms that were identified as *Phyllobothrium* sp. and *Dinobothrium* sp. Brown and Threlfall (1968a, b) reported metacestodes of additional species: *Scolex polymorphus*, *Pelichnobothrium speciosum* and *Nybelinia* sp. from *Illex illecebrosus* in the Newfoundland area. *Loligo pealeii* is rare in the maritime provinces of Canada, although it is the common squid of Cape Cod, Massachusetts. Examination of *L. pealeii* during the summer months of 1974, 1975, 1976 at the Marine Biological Laboratory has disclosed heavy infection with cestode plerocercoids and eight species have been recognized. The squids were taken in the Woods Hole area by the Supply Department of the MBL. During the summer of 1974, a group from the Duke University Medical Center under the direction of Professor T. Narahashi was engaged in neuropharmacological studies using the giant axons of the squids. After the elements essential for the neural investigation were removed, the bodies of the squids were turned over to me for parasitological examination. I wish to acknowledge the kindness of members of the group with special thanks to Dr. Brij Srivastav and Mr. John Starkus.

Between May 25 and August 20, 1974, 128 squids were examined. The digestive tracts contained fragments of food material, bits of fishes, crustaceans, and other remains. In early summer, the stomach and caecum were often stuffed with balls of compacted algae, identified by Dr. Joseph Ramus of Yale University as tips of *Codium fragile*, a species with universal distribution that has appeared in the New England area in the past ten years. Dissection of the squids yielded four species of tetraphyllidean metacestodes and four species of tetrarhynchidean metacestodes, either free in the lumen, attached to the surface, or embedded in the wall of the stomach and caecum. In addition, metacercariae of two species of digenetic trematodes were found; one is a hemiurid which was encysted in the wall of the stomach and the other is a member of the family Didymozoidae with specimens embedded in the walls of both the stomach and caecum.

The worms were studied alive and killed either by the shaking method of Looss or by pressure under a coverglass, depending on the size and texture of the specimen. Fixation was made by the solution of Duboscq-Brasil and the plerocercoids were stained with Ehrlich's haematoxylin, Mayer's paracarmine or Semichon's acetic acid carmine. The Semichon method is somewhat capricious, but when successful, the results are striking, especially in the staining of the hooks of the tetrarhynchs. The metacestodes are described and tentatively assigned to taxonomic groups. Specific descriptions of cestodes are based primarily on sexually mature, strobilate specimens, and since metacestodes are comparable solely with the scolices of adults, determination can be positive only in special cases where features like hook-patterns of tetrarhynchid species are characteristic. The number of plerocercoids present in a squid varied from one to more than one hundred. The small, slightly developed specimens with an apical and four simple, circular suckers (Figs. 9, 10), recognized as *Scolex pleuronectis* O. F. Mueller, 1788, probably identical with *Scolex polymorphus* Rudolphi, 1819, were very common and more than 100 were taken from the stomach and caecum of a single squid. They were free in the lumen or loosely attached to the wall. The larger specimens were present in small

numbers, usually less than five. As rule, they were firmly attached to the gut wall or encapsulated in host tissue. When embedded, they could be released only after the cyst wall was cut away.

At my request, representative examples of the several kinds of plerocercoids have been studied by Professor Louis Euzet, Université de Montpellier, France. For his kindness and generosity in examining the specimens and suggesting possible systematic allocations, I express deep appreciation and esteem.

From study of the plerocercoids it is clear that the material contains four different kinds of phyllobothrids and four species of tetrarhynchs. Since definite identification cannot be made, the species are assigned arbitrary numbers and described. Possible taxonomic considerations are discussed.

The specimens described in this report have been deposited in the platyhelminthic collection of the American Museum of Natural History.

Descriptions

TETRAPHYLLIDEA

The tetraphyllidean cestodes have three-host life cycles. The first hosts are copepods in which the oncospheres undergo metamorphosis to form procercoids. Procercoids, in their copepod hosts, are ingested by a second intermediate host, another invertebrate or small fish in which they develop into plerocercoids. Plerocercoids are solid bodied post-larval stages, in which the anterior end may be invaginated and the posterior end may have the beginnings of strobilation. Four species have been taken from *Loligo pealeii* at Woods Hole.

SPECIES NUMBER 1. *Phyllobothrium loliginis* (Leidy, 1887) Linton, 1897. Figures 1, 2.

In the present study, *P. loliginis* was found in 12 squids, free or attached to the wall of the stomach or caecum. Two representative specimens are shown in Figures 1 and 2.

The specimen in Figure 1 is 32 mm long and 3.65 mm in greatest width. The *pars antica* is 17 mm long; the *pars bothridialis* is 2 mm long and the *pars proliferus* is 15 mm long. The scolex is 4 mm wide, the stem is 1.9 mm wide and the apical sucker is 0.18 by 0.20 mm in diameter. The bothridia are sessile, with crumpled and folded edges, 1.5 to 1.8 mm long and 0.09 to 1.00 mm wide. The bothridial suckers are circular to oval and 0.040 to 0.046 mm in diameter. The *pars postica* is 15 mm long and tapers to a point posteriorly. The major excretory tubules are conspicuous. The pore is terminal with a short common duct which divides to form the primary collecting ducts that extend forward ventrally on each side of the body. They enter the scolex, extend around the periphery of the bothridia of that side and pass posteriad, dorsal in location, beside or crossing the ascending tubules. Fluid passes anteriad in the dorsal tubules and posteriad in the ventral ones.

Figure 2 is of the somewhat flattened scolex of a specimen 14 mm long and 2.68 mm in greatest width. In it the *pars antica* is 6 mm long, the *pars bothridialis* is 1.6 mm and the *pars proliferus* is 4.40 mm long. The *pars postica* is 8 mm long. The scolex is 3.10 mm wide; the stem is 1.6 mm wide. The bothridia are separate, slightly stalked, 1.2 to 1.5 mm long and 0.08 to 1.00 mm wide. The apical sucker

is 0.19 by 0.20 mm in diameter and the bothridial suckers are oval, 0.04 to 0.046 mm in diameter.

Leidy (1887) described plerocercoids from the northern squid, identified as *Ommastrephes illecebrosa* [= *Illex illecebrosus* (Lesueur, 1821) Steenstrup, 1880], taken at Mt. Desert, Maine as *Taenia loliginis*, and he (1891) predicated that the larva was the scolex of a species in the genus *Tetrabothrium* Rudolphi, 1819 or *Phyllobothrium* van Beneden, 1849. Linton (1897a) reported the worms from the stomach of *O. illecebrosa* taken at Provincetown, Massachusetts, and assigned the species to *Phyllobothrium*. Linton (1901) reported three specimens from the stomach of the silver hake, *Merluccius bilinearis*, collected 11 July, 1900. His figure 231 is indeterminate, but figure 232 is a clear representation of the scolex of *P. loliginis*. Linton (1922b) recorded collection of *P. loliginis* from *O. illecebrosa* and *Loligo pealeii* at Woods Hole, Massachusetts, and the recovery of the plerocercoids from the stomachs of hundreds of fishes examined in the previous twenty years at the laboratory of the U.S. Bureau of Fisheries in Woods Hole. Many of the examinations were made by Vinal N. Edwards. The stomachs typically contained squid, fish, and crustaceans, and it appeared that the plerocercoids were in squid when ingested. Summarizing the report Linton stated, p. 14, "Selachians in which the larval form, *Phyllobothrium loliginis*, was found were *Mustelus canis*, *Squalus acanthias*, *Raja laevis*, and *Raja ocellata*. In no case had proglottides begun to develop. If either of these four species of selachians ever serves as the final host of this cestode the fact is not indicated by any of the data at hand. On the contrary, sufficient numbers of these hosts were examined in the months of July, August, September, October and November without finding any adult cestode that could be linked up with this form to make it appear very improbable that *P. loliginis* can reach adult stage in any of these four selachians.

"There is no reason whatever for thinking that *P. loliginis* ever attains maturity in any teliost (*sic*). It seems, however, that this larval cestode can resist the digestive juices of a great variety of hosts for some time. Hence it doubtless often happens that, before this larval *Phyllobothrium* has reached a true final host, such, for example, as the mackerel shark, or maneater shark, it has sojourned for a shorter or longer time in the alimentary canal of one or more species of selachian, teliost (*sic*) or squid."

Linton (1922b) described *Phyllobothrium tumidum* n. sp., from the maneater and mackerel sharks, *Carcharodon carcharias* and *Isurus dekayi*, and postulated that it may be the mature stage of *P. loliginis*. The presumption was based on similarity in form and details of structure of the scolex. He noted, p. 15, "In the structure of the bothria and auxiliary suckers, and in the axial portion of the scolex, there is close agreement." One feature which he found disconcerting was the narrow neck region posterior to the bothridia in *P. loliginis*. But this difficulty poses no problem, since the so-called neck region may be contracted and broad as shown in Figure 1 of the present study. Linton noted that the cestodes from *C. carcharias* were mature with detached gravid proglottids in the intestine, whereas "There were no ripe segments" in *I. dekayi*. This observation suggests that *P. tumidum* is a normal parasite of the maneater shark, but that the cestode does not mature in *I. dekayi*. There are strong indications that *P. tumidum* may be the mature stage of *P. loliginis*, and if so the specific name, *tumidum*, will be reduced to a synonym.

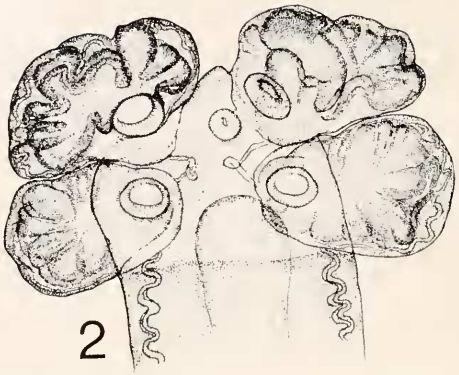
The use by Linton of the term bothria for the holdfast organs of *P. loliginis* is unfortunate. Bothria are middorsal and midventral longitudinal grooves on the scolex of pseudophyllidean cestodes. The corresponding structures of the tetraphyllidean cestodes are bothridia, four leaflike outgrowths of the surface, continuous with the underlying tissues. These organs are very mobile and serve for locomotion as well as for adhesion.

Guiart (1933) described and figured a plerocercoid from the mantle of *Ommastrephes sagittatus* taken by Dr. Harant in the Mediterranean. He predicated, p. 465, "A n'en pas douter, il s'agissait de la larve pléroceroide du *Phyllobothrium loliginis* décrit par Leidy en 1887 et en 1890, chez *Ommastrephes illecebrosa* des côtes des États-Unis et revu chez le même hôte par Linton en 1897." Guiart noted that Leidy (1887) had described the plerocercoid as 12.7 mm long and 1.00 mm wide, whereas in the (1891) account Leidy reported larger specimens, as much as 25.5 mm long and 2 to 3 mm wide. Guiart reviewed the description by Linton (1897a) and observed, p. 467, "Une larve si non identique, du moins très voisine, a été décrite en 1929, par R. Dollfus; elle avait été trouvée à Arcachon, par Cuénot, dans la paroi de l'estomac de *Loligo loligo*. Elle mesurait environ 1 cm de long et présentait une tête encore plus caractéristique: en effet, les bothridies sont fortement plissées avec une assez grosse ventouse accessoire en avant et une cinquième ventouse à l'apex du scolex (Fig. 5)." Guiart continued, p. 467, "Justement, j'avais reçu autrefois de M. Hérubel un flacon portant l'inscription suivante: 'parasites de *Loligo vulgaris* recueillis par M. Hérubel, à Arcachon, en Mai 1903'. Les parasites étaient encore des larves plérocercoides à corps longuement lancéolé, mais il suffisait d'un examen grossier pour se rendre compte qu'on se trouvait en présence de deux formes différentes, dont l'une, représentée par 8 exemplaires measurant de 10 à 45 mm de longueur, est bien la larve de *Phyllobothrium* sp. trouvée par Cuénot et publiée par Dollfus. La plupart des examplaires mesurent 23 à 30 mm de longueur; la tête mesure 2 mm de longueur sur 2 mm 5 de largeur; l'extrémité du corps, lancéolée, mesure 2 mm 5 dans la plus grande largeur. Les bothridies ont un diamètre moyen de 1 mm. La ventouse accessoire cupuliforme occupe la partie antérieure des bothridies. Enfin l'extrémité antérieure du scolex présente une ventouse."

Commenting on the proposal by Linton (1922b) that *Phyllobothrium tumidum* may be the adult stage of *P. loliginis*, Guiart stated, p. 468, "Il est possible que le *Phyllobothrium tumidum* Linton, 1922 soit la forme adult du *Phyllobothrium loliginis*, mais le fait n'est nullement démontré. En effet, l'aspect du scolex de *P. tumidum* est totalement différent de celui du scolex de *P. loliginis:* la partie antérieure bombée n'existe pas chez la larve et les bothridies rappellent plutôt celles de *Ph. lactuca* que celles de la larve du Calmar. On ne saurait donc actuellement avoir une opinion ferme sur cette question."

Phyllobothrium tumidum Linton, 1922 was redescribed by Riser (1955) on specimens from *Lamna ditropis* Hubbs and Follett taken at Monterey, California and from *Carcharodon carcharias* (Linn.) taken at La Jolla, California. He observed, p. 273, "The species differs from all other members of the genus in that the phyllidea arise posteriorly from the lateral walls of the scolex leaving an anterior cone-like projection visible, the vitellaria extend almost to midline, and the ventral wing of the ovary is absent."


1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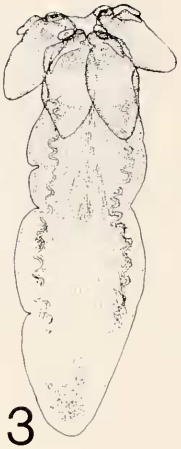
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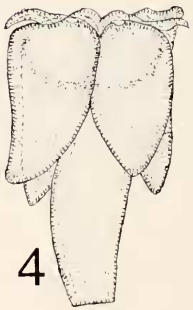
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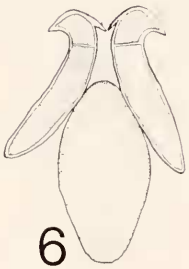
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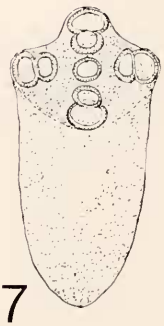
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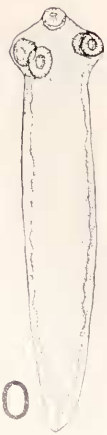
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Squires (1957) reported phyllobothrid and dinobothrid plerocercoids from *Illex illecebrosus* taken in the area between the Grand Banks and the Canadian coast of Newfoundland. Stomach contents of about 1500 specimens were examined in the periods March to November in the years 1946 to 1952. The plerocercoids of *Phyllobothrium* sp. were free in the stomach, caecum, and rectum and often emerged through the anus; those of *Dinobothrium* (*sensu lato*) were often encapsulated in the walls of the caecum and rectum, mostly in the spiral part of the caecum. The phyllobothrids were mainly large, about 20 mm long; the dinobothrids were small, not more than 2 mm long. Infestation by *Phyllobothrium* sp. was greater in small squids taken on the Banks early in the season and gradually diminished as the squids entered inshore waters. The small squid fed mostly on euphasid crustaceans; larger squid on fishes. Incidence of infection by phyllobothrids varied from 35 to 20% from May to November, by dinobothrids it increased from 15 to 75% during this time.

Dollfus (1958) gave a list of the tetraphyllidean larvae that have been reported from cephalopods of the Mediterranean and European Atlantic coasts. He stated, p. 65, "Dans l'estomac, à Arcachon (Gironde), L. Cuénot (in R. Ph. Dollfus 1929) a trouvé un plérocercoide de *Phyllobothrium*. Des spécimens identiques, trouvés aussi chez *L. loligo* (L.), sont conservés au Musée de Münich (voir Ch. Joyeux et R. Ph. Dollfus 1931; R. Ph. Dollfus 1931) et René Legendre en a trouvé plusieurs individus dans l'intestin et la paroi du manteau à Concarneau (Finistère). La même larve que celle de Cuénot a été récoltée en 8 examplaires chez le même hôte, à Arachon, par Marcel Herubel (in Jules Guiart 1933). Cette larve est'sinon identique du moins très voisine', selon Guiart (1933) de *Phyllobothrium loliginis* (J. Leidy 1887), décrit aux États-Unis par J. Leidy (1887, 1891) et Edwin Linton (1897); elle correspond presque sûrement, d'après Linton (1922) "à *Phyllobothrium tumidum* Edwin Linton 1922, identifié adulte chez *Isurus* à Concarneau (Finistère) et à Sète (Hérault)." Williams (1968) reviewed the taxonomy, ecology and host-specificity of some Phyllobothriidae, with a critical revision of *Phyllobothrium*.

The most comprehensive and detailed studies of the Tetraphyllidea are contained in the thèses of Euzet (1959). As noted earlier, he fed eggs of *Phyllobothrium lactuca* from *Mustelus canis* to copepods and removed active procercoids. The summary of the thesis includes the statement, p. 249, "J'ai essayé d'élucider le cycle évolutif encore inconnu de ces Cestodes. D'après mes expériences, les

FIGURES 1–10. Larval stages of marine metacestodes. The specimens depicted in these figures are deposited in the platyhelminth collection of the American Museum of Natural History under the assigned numbers. Figure 1: *Phyllobothrium loliginis* (Leidy, 1887), *provis.*, specimen, 32 mm long (No. 890). Figure 2: *P. loliginis*, flattened scolex, 3.4 mm wide, specimen 14 mm long (No. 891). Figure 3: *Dinobothrium septaria* van Beneden, 1889 *provis.*, specimen 2.75 mm long (No. 892). Figure 4: *D. septaria*, specimen 0.28 mm long (No. 893). Figures 5 and 6: copies of Figures 10 and 11 in Linton (1897), described as *Thysanocephalum* sp., a larval cestode, 1 mm long, from *Illex illecebrosus* taken at Provincetown, Massachusetts. Dollfus (1936) identified the specimen as *Dinobothrium plicitum* Linton, 1922; probably a synonym of *D. septaria*. Figure 7: *Ceratobothrium xanthocephalum* Monticelli, 1892, *provis.*, specimen 0.56 mm long (No. 894). Figure 8: *C. xanthocephalum*, specimen 2.75 mm long (No. 895). Figure 9: *Scolex pleuronectis* O. F. Mueller, 1788, *provis.*, specimen with invaginated scolex, 0.5 mm long (No. 896). Figure 10: *S. pleuronectis*, specimen extended, 1.2 mm long (No. 897).

Tétraphyllides ne dovient pas posséder de coracidie nageante. Tous les oeufs que j'ai élevés sont morts, 15 à 20 jours après le ponte sans donner cette forme larvaire. J'ai réalisé expérimentalement l'infestation des Copépodes planctonique: *Acartia clausi* Giesb. et *Acartia discaudata* Giesb., avec des oeufs de *Phyllobothrium lactuca* P.-J. Van Ben., 6 jours après l'infestation, j'ai constaté dans la cavité générale des Copépodes des procercoides mesurant de 200 à 400 μ de long. Cette expérience montre pour la première fois les procercoides des Tétraphyllides de sélachiens semblent évoluer dans les Copépodes."

Euzet (1959) described *Phyllobothrium tumidum* from *Isurus oxyrhynchus* taken at Sète in the Mediterranean and at Concarneau on the Brittany coast of France. After studying specimens of the present collection, including those represented in Figures 1 and 2, he reported by letter, "Bien que l'on n'ait aucune preuve expérimentale je suis persuadé que ces formes correspondent à des postlarves de *Phyllobothrium tumidum* Linton, 1922 que l'on rencontre chez les Isuridae."

There is much evidence that *Phyllobothrium loliginis* is a parasite of squids on European as well as American coasts. The final host is almost certainly one or more of the mackerel sharks, Isuridae, wide-ranging fishes that occur in all oceans.

SPECIES NUMBER 11. *Dinobothrium septaria* P. J. van Beneden, 1889, *provis.* Figures 3–6.

Only five individuals of this species were found. They were embedded in the wall of the stomach and caecum. The largest and most representative specimen is shown in Figure 3. It is somewhat flattened and the upper bothridia are spread apart, whereas the lower pair of bothridia extend posteriad and their median edges are almost contiguous in the midline. This metacestode is 2.85 mm long. The *pars antica* is 1.33 mm long; the *pars postica* is 1.52 mm long and 0.85 mm wide. The *pars bothridialis* is 0.57 mm long and 0.57 mm wide. The *pars proliferus* is 0.76 mm long and 0.76 mm wide. The anterior face of the scolex is flattened, 0.72 mm wide. There is no myzorhynchus, but the anterior ends of the bothridia are surmounted by muscular crests or bolsters with two fingerlike lobes at each lateral end. The bothridia are sessile, oval, concave, attached by the anterior ends with the posterior ends free and thin. The bothridia bear exceedingly fine spines, and spines three to four times as large are present on the neck region of the *pars bothridialis*. Each bothridium bears an acetabulum, situated near the anterior end, oval in shape and 0.072 by 0.03 to 0.04 mm in diameter. A small specimen is shown in Figure 4. In it the scolex is 0.28 mm wide. The smallest specimen recovered, stained and mounted, is 0.23 mm wide, and it is clear that the plerocercoids increase greatly in size when encysted. The squids are truly intermediate and not mere transfer hosts.

The genus *Dinobothrium* P. J. van Beneden, 1889 was erected to contain *Dinobothrium septaria* van Beneden, 1889, from the mackerel shark, *Lamna cornubica* [= *Lamna nasus* (Bonnaterre, 1788)]. The original description was based on immature worms, and the species was redescribed by Lönnberg (1892, 1899) and by Scott (1909) on specimens from the same host, the porbeagle shark, *L. cornubica*. Certain species assigned to *Dinobothrium* have been transferred to other genera and other species have been suppressed as synonyms of *D. septaria*.

Linton (1922a) described two new species of *Dinobothrium*. Immature specimens taken September 1, 1903 from the spiral valve of a small maneater, *Carcharodon carcharias*, undescribed, but listed as "*Dinobothrium septaria* Linton (*in ms*)" by Sumner, Osburn and Cole (1913), were described as *Dinobothrium plicitum* n. sp. There were ten scolices but the strobilas were immature. In the figure, the bothridia were disposed in cuplike fashion. The scolex was 2.00 mm to 2.50 mm in breadth. Other specimens, taken June 20, 1920 from the spiral valve of a basking shark, *Cetorhinus maximus*, were described as a new species, *Dinobothrium planum*. The scolex of the largest individual was 10 mm broad, 5 mm thick and 8 mm long. In three other specimens the scolices were 6 mm broad and 4 mm thick. Southwell (1925) compared descriptions of *D. septaria* and *D. plicitum*, and referring to *D. plicitum*, declared, p. 170, "This species is inseparable from *D. septaria* van Beneden." Woodland (1927) and Perrenoud (1931) redescribed *D. septaria* and both suppressed *D. plicitum* as a synonym of *D. septaria*. Sproston (1948) included *D. plicitum* as a synonym of *D. septaria* and Baylis (1950) stated, p. 96, "The writer agrees, in the main, with the synonymy given for this species by Sproston." But in describing *D. plicitum* Baylis noted, p. 98, "The status of this species is very uncertain." Linton's (1922a) original material from *Carcharodon carcharias* was immature, and his description contains nothing of diagnostic value concerning the anatomy of the strobila. Guevara (1945) described the species of *Dinobothrium* taken on the Spanish coast. Yamaguti (1952) found *D. planum* in *Cetorhinus maximus* in Japan, and erected a new genus, *Gastrolecithus* to receive the species which was designated, *Gastrolecithus planus* (Linton, 1922).

Euzet (1955) reviewed the history of the genus *Dinobothrium*. He examined the specimens of Sproston, of Baylis, and those from other collections, and gave a revised account of the genus. For *Dinobothrium paciferum* Sproston, 1948, he erected a new genus, *Recesium*. *Gastrolecithus* Yamaguti, 1952 was named type of a new family, Gastrolecithidae. Concerning *D. plicitum*, he predicated, p. 176, "Une espèce reste douteuse, c'est *Dinobothrium plicitum* Linton, 1922. Le ver était immature et, la différence entre les diverses espèces étant surtout basée sur l'anatomie, il ne peut être mis en synonymie avec l'une ou l'autre. Seule, la récolte chez *Carcharodon carcharias* d'individus adultes pourait trancher la question." But *D. plicitum* may be a synonym of *D. septaria*, and it is possible that *C. carcharias* is not a natural host and that the parasite does not mature in it.

Linton (1897a) reported on a larval cestode. His account, p. 792 reads, "*Thysanocephalum* sp. (Larva). (Plate 11, figs., 10–11). One small specimen, 1 mm in length, from the stomach of the squid, (*Ommastrephes illecebrosus*). Collected, August 28, 1886, at Woods Hole, Massachusetts. The squids were caught at Provincetown, Massachusetts (No. 4815, U.S.N.M.) The specmen is the young of my genus *Thysanocephalum*, and presumably of the species *T. crispum*. Only the scolex was present." There was no description of the specimen, but it was depicted in Plate 11, figs. 10 and 11. The two drawings are reproduced (Figs. 5 and 6 in the present account) and might have been made from a small individual taken in the current investigation. The plerocercoid clearly belongs to Species Number 11. It is very similar and possibly identical with the metacestodes taken by Legendre from squids at Concarneau, France and described by Dollfus (1936) as

Dinobothrium plicitum Linton, 1922. Dollfus (1936) gave a detailed description, with figures, of these plerocercoids and concluded, p. 525, "Signalé deux fois seulement dans la paroi intestinale de *Todaropsis eblanae* (R. Ball) à Concarneau (Finistère) et une fois dans l'estomac d'un *Ommatostrephes illecebrosus* Verrill, à Princetown (sic) Massachusetts. Nous avons préféré conserver le nom spécific de *plicitum* car nous ne sommes pas convaincus de l'identité de cette espèce avec *D. septaria* (voir p. 94)". Baylis (1950) noted that Dollfus (1936) assigned the plerocercoids from *T. eblanae* to *Dinobothrium plicitum* and Sproston (1948) predicated, p. 74, "The recent findings of Dollfus (1936, pp. 523-5) leaves no doubt that the intermediate hosts of *D. septaria* are cephalopods of the family Ommastrephidae." As noted earlier in this report, Squires (1957) found plerocercoids of *Dinobothrium* sp. in squid, *Illex illecebrosus*, in the Newfoundland fishing area. There was no description but the measurement, "not more than 2 mm long", and the figures denote identity with the plerocercoids described by Linton (1897a, 1922a). There is strong probability that the dinobothrid metacestodes from cephalopods on the American and European coasts are conspecific. The observation by Linton (1922a) that they mature only in large, oceanic selachians, which frequent both areas, supports such a postulate.

In the sixth edition of his *Enumération des Cestodes du plancton et des Invertébrés marins*, Dollfus (1964) reviewed the information on plerocercoids from cephalopods. He gave a more detailed account of the morphology of the metacestodes assigned to *D. plicitum* and republished the figures from his (1936) report. His discussion, p. 359, states, "Si l'on s'en tient seulement aux caractères du scolex (et l'on y est obligé lorsqu'il s'agit du plérocercoide), on distingue parmi les spécimens de *Dinobothrium*, d'après les descriptions et figures publiées, deux groupes, différant par un caractère externe très apparent. Chez les spécimens du premier groupe, les deux angles antérieurs du rebord de chaque bothridie se terminent par une pointe courte, rigide, "hook-like" (pour employer l'expression de Linton), à peu près perpendiculaire au plan frontal. Chez les spécimens du second groupe, ces "pseudo-hooklets" n'existent pas.

Le premier groupe d'exemplaires appartient à *Dinobothrium plicitum* Edw. Linton [1922, p. 2–5, 10, pl. 1, fig. 1, pl. II, fig. 4–6, de *Carcharodon carcharias* (L.) à Woods Hole, Mass.]. Le second groupe d'exemplaires est representé par *D. planum* Edw. Linton 1922, [p. 2, 5–8, 10, pl. 1, fig. 2–3, pl. III-IV, fig. 7-13, de *Cetorhinus maximus* (Günner), à Menemsha Bight, Mass.]."

The relation between *D. septaria* and *D. plicitum* remains uncertain. Clarification of the status of the plerocercoids from *L. pealeii* may be derived from bionomic considerations. Euzet (1959) discussed host-parasite relations. He declared, p. 242, "Je suis persuadé que la spéificité parasitaire des Cestodes est plus large," and on the same page, "Une espèce de Tétraphyllide n'a encore été rencontré que chez une espèce de Sélachiens." In correspondence he has suggested that these plerocercoids are probably referable to *Dinobothrium septaria*, rather than to one of the species from *Cetorhynchus maximus*, since the latter species is a plankton feeder and unable to eat the larger cephalopods. There is a possibility, however, that the cephalopods, like the basking sharks, may have acquired the larvae by ingestion of small crustaceans in the plankton. But *Lamna nasus*, a host of *D. septaria*, occurs at Woods Hole, and the suggestion of Euzet becomes almost a certainty.

SPECIES NUMBER III. *Ceratobothrium xanthocephalum* Monticelli, 1892, *provis.* Figures 7, 8.

Small plerocercoids, recognizable as *Scolex bothriis bilocularis* G. R. Wagener, 1854, were common and scores were taken. Small and larger specimens are shown in Figures 7 and 8. The specimen shown in Figure 7 is 0.56 mm long and the scolex is 0.26 mm wide. The apical sucker is 0.056 mm in diameter and the *pars bothridialis* is very short. Each of the bothridia has a simple border and a bipartate lumen. The overall length of the bothridia is 0.09 to 0.11 mm. The central part of each bothridium is 0.035 to 0.056 mm in diameter and the distal part is 0.05 to 0.07 mm in diameter. Each is somewhat flattened and constricted at the junction of the two parts. Figure 8 shows a larger specimen in which the anterior end is flattened and the bothridia are separated. The *pars antica* is 0.90 mm long; the *pars postica* is 1.85 mm long and 0.85 mm wide. In the *pars bothridialis*, the median peduncle is 0.36 mm long and 0.52 mm wide. The *pars proliferus* is 0.57 mm long and 0.67 mm wide. The apical sucker is 0.11 mm in diameter. The bothridia are 0.36 to 0.042 mm long, with the two sections flattened and slightly constricted at the junctions. The medial portion measures 0.06 to 0.11 mm in diameter and the distal portion 0.20 to 0.28 mm in diameter. There are four small patches of red pigment in the wall posterior to the bothridia.

Linton (1889a, p. 464, Pl. II, figs. 1–12) described *Phyllobothrium thysanocephalum* from the tiger shark, *Galeocerdo tigrinus*. Similar and presumably identical specimens, from an unknown host, in the British Museum were described by Monticelli (1889) as *Phyllobothrium crispatissimum*. Linton (1890, p. 823) erected the genus *Thysanocephalum* with *Thysanocephalum crispum* (= *thysanocephalum*, renamed) as type. Linton (1901, p. 426) listed *T. crispum* from the spiral valve of *G. tigrinus* and p. 430, described *Thysanocephalum ridiculum* n. sp., from the mackerel shark, *Isurus dekayi*. Euzet (1959) corrected the name of the species from the tiger shark to *Thysanocephalum thysanocephalum* (Linton, 1889b), proposed a new subfamily, Thysanocephalinae, in the family Phyllobothriidae, and suppressed *Thysanocephalum rugosum Chandler*, 1942 as a synonym of *T. thysanocephalum*.

Monticelli (1892) described *Ceratobothrium xanthocephalum* n. g., n. sp., from the spiral valve of *Lamna cornubica* (= *L. nasus*) taken in the Mediterranean. Euzet (1959) redescribed *C. xanthocephalum* from specimens taken in *Isurus oxyrhynchus* at the marine laboratories of Sète on the Mediterranean and Concarneau on the Atlantic coast of Brittany, France. He suppressed *T. ridiculum* Linton, 1901 from *Isurus dekayi* as a synonym of *C. xanthocephalum*. Independently, Yamaguti (1959) listed *T. ridiculum* as identical with *C. xanthocephalum* and reported the parasite from *Isurus glaucus* in Japan.

The plerocercoids of Species No. III agree substantially with the descriptions of *C. xanthocephalum*, and while specific determination cannot be based solely on the scolex, they show considerable agreement with the figures of *T. ridiculum* as given by Linton (1901, Pl. XXVII, figs. 294, 295).

SPECIES NUMBER IV. *Scolex pleuronectis* O. F. Mueller, 1788, *provis.* Figures 9, 10.

These plerocercoids were very common and numerous in *L. pealeii* at Woods Hole. Often as many as one hundred were present in a single squid. They con-

form to the classical representation and cannot be assigned to any genus or species. Fixed, stained, and mounted specimens are shown in Figures 9 and 10. Figure 9 is of a specimen in which the anterior end is invaginated; it is 0.50 mm long and 0.23 mm wide. Figure 10 is of a specimen 1.2 mm long and 0.20 mm wide. The apical sucker is 0.07 mm in diameter and the bothridia are represented as simple, circular suckers, 0.09 to 0.10 mm in diameter.

Under the designation, *Scolex pleuronectis*, there has been recorded a variety of larvae, all apparently tetraphyllidean, taken from a large list of invertebrates and the intestine of fishes that had ingested the former hosts. Linton (1901) reported *Scolex polymorphus* from 28 species of teleost fishes examined at Woods Hole. Reporting on parasites of fishes taken at Beaufort, North Carolina, he observed, (1905, p. 326) "The larval cestodes, doubtless representing several different genera, recorded in Parasites of the Woods Hole Region under the name *Scolex polymorphus*, were found in 34 of the 59 Beaufort fishes examined (Figs. 76–79). As at Woods Hole, these forms are found not only in the alimentary tracts of their hosts, but also in the cystic ducts of several. They are almost never absent from the cystic duct of *Cynoscion regalis*. In all cases where these worms have been obtained from the cystic duct and from the intestine of the same fish, those coming from the cystic duct are larger, plumper, and more opaque than those from the intestine. Some of the older larvae suggested the genera *Calliobothrium*, *Acanthobothrium*, and *Phoreiobothrium*."

Discussing the group of plerocercoids known as *Scolex pleuronectis*, Wardle and McLeod (1952, p. 231) predicated, "It is probable that these larvae represent a number of tetraphyllidean species." Euzet (1959, p. 228) reported, "On recontre *Scolex pleuronectis* dans le tube digestif de nombreux Téléostéens marins aussi chez un certain nombre d'invertébrés: Cténophores (*Scolex acalepharum* M. Sars, 1845; *Tetrastoma playfairi* Forbes, 1849; Vers Nemertes (*Scolex*); Mollsuques Lamellibranches (*Scolex*); Mollusques Céphalopodes (*Scolex pleuronectis* O. F. Müller); Crustacés Copépodes (*Plerocercoides aequoreus* Wündsch et *Plerocercoides armatus* Wündsch, 1912); Crustacés Décapodes (*Scolex paguri bernhardi* K. M. Diesing, *Scolex carcini maenadis* Vaullegeard, *Echencibothrium mouchetae* R.-P. Dollfus). Cette larve très polymorphe même dans un même hôte, est très difficile à décrire et il est certain que les larves de différents Tétraphyllides ont été groupées sous un même nom. Ces parasites sont en général aplatis, lancéolés vers l'arrière et présent, à la partie antérieure, 4 bothridies et une ventouse apicale."

TETRARHYNCHIDEA

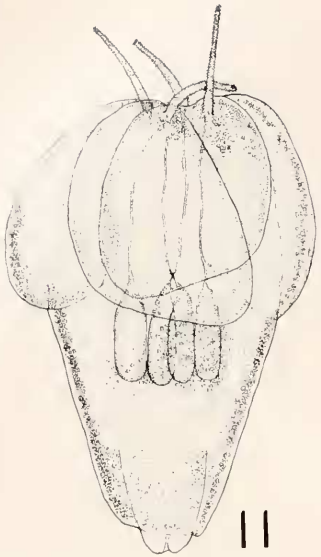
Tetrahynchid metacestodes are post-larval forms that have lost their blastocysts and, accordingly, are not directly comparable to the plerocercoids of the Tetraphyllidea. For this stage, Dollfus (1942) proposed the designation, plerocercus.

SPECIES NUMBER V. *Nybelinia bisulcata* (Linton, 1889) Dollfus, 1929, *provis.* Figures 11, 12.

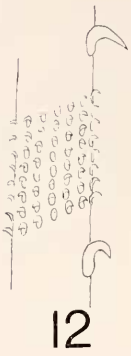
These worms were embedded in the walls of the stomach and caecum of squids. The cysts were tough, fibrous, and the metacestodes were released only when the

cyst was dissected away. The specimens are ovate, wider anteriorly. The anterior end is rounded, often somewhat flattened. The specimens are very uniform in size, the total length varies from 3.40 to 3.90 mm and the width from 2.20 to 2.40 mm. The greatest width is at the posterior portion of the bothridia, termed pseudobothridia by certain authors. In length, the *pars bothridialis* measures 1.80 to 1.90 mm and the *pars postbothridialis* is about the same length. The *pars bulbosa* measures 0.60 to 0.80 mm in length and the anterior end is partially overlapped by the *pars bothridialis*. The region between the *pars bulbosa* and appendix is 0.40 to 0.50 mm in length. The *pars post bulbosa* is 0.60 to 0.75 mm in length, and the length of the velum is determined by the degrees of retraction of the *appendix*. The posterior end of the appendix bears the excretory pore; there is a short vesicle and the collecting ducts pass forward on either side of the structure. The tentacular bulbs are banana-shaped, bent slightly outward at the middle. They measure 0.55 to 0.75 mm in length and 0.20 to 0.25 mm in width. The tentacle-sheaths are longer than the bulbs or the tentacles. The tentacles are 0.80 to 0.85 mm long when fully extended. Without hooks, they are 0.08 to 0.09 mm wide at the base and 0.03 to 0.35 mm wide at the tip. They do not have a special armature at the base. The hook arrangement is homeoacanthous (Fig. 12). The hooks are solid; they measure 0.018 to 0.021 mm long and 0.007 to 0.008 mm wide at the base. Those near the base of the tentacles are slightly shorter, abruptly recurved, without extended bases; proceeding toward the tip the hooks are slightly longer, with sharper points and broad elongate bases. The hooks are set in diagonal spiral rows, with six or seven visible in each row. The rows are separated by intervals, each about one-half the length of the hooks, and appear to cross like the letter X, when the plane of focus in shifted from one side to the other. There are about 30 rows of hooks. The tegument of the body bears fine, sharply pointed, flat spines, 10 to 14 μ long and 3 μ wide. In addition, the edges of the bothridia are thickened and bear longitudinal rows of closely set bristles, 25 to 30 μ long. They are uniform in diameter and form a fringe that resembles cilia. The body wall consists of circular, longitudinal and oblique muscle fibers and below the wall the parenchyma is filled with secretory cells. The secretion appears in the form of vesicles, 12 to 20 μ in diameter, partially filled with fluid or scores of minute granules.

Cuvier (1817) described tetrarhynchid larvae from the turbot, (= *Scophthalmus maximus*) *as Tetrarhynchus lingualis*. Similar larvae from the mantle and stomach of *Sepia officinalis* taken at Nice, France were identified by Wagener (1854) as *Tetrarhynchus lingualis* Cuvier, 1817. Vaullegeard (1899) described metacestodes from connective tissue cysts in the wall of the digestive tract of *Octopus vulgaris*, taken off the coast of Brittany as *Tetrarhynchus bisulcatum* Linton, 1889. The specimens were 3 to 4 mm long, the tentacular bulbs measured 0.34 by 0.11 mm, and the hooks were 0.020 mm long. Tentarhynchid larvae were taken, mainly by Professor Cuénot, from the stomach wall of *Loligo loligo*, *Sepia officinalis*, and *Sepia fillilouxi* at Arcachon, France and studied by Dollfus (1929). He described the specimens from *Sepia fillilouxi* as *Nybelinia lingualis* (Cuvier). He declared that the plerocercoids from cephalopods do not belong to the genus *Tetrarhynchus*, but to the genus *Nybelinia* Poche, 1926, a new name for the genus *Aspidorhynchus* Molin, 1858, preoccupied. Dollfus (1930) discussed the "groupe *lingualis-bisulcatus*" and stated, p. 208, "Ne m'occupant pas ici d'une révision des espèces, je



11



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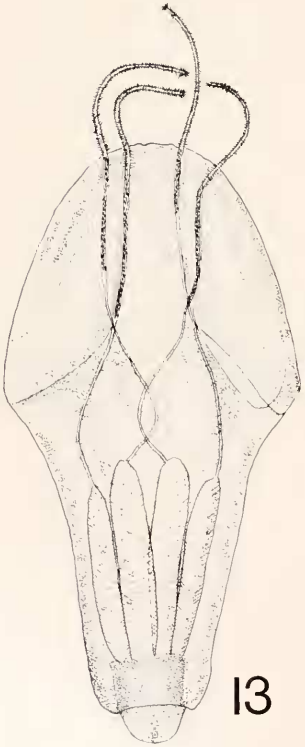

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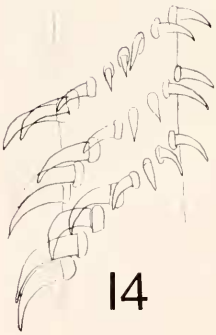

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16

n'examinerai pas si *bisulcata* (Linton) tombe, ou non, en synonymie avec *Linguale* (Cuvier) ou n'en est qu'une variété." Dollfus (1942) listed the synonymy of *Nybelinia* and divided the genus into two subgenera: *Nybelinia* and *Syngenes*. *Nybelinia lingualis* (Cuvier) was designated type of the subgenus *Nybelinia* and a key was formulated to the ten species recognized as valid. In the Key, p. 146:
"B. Formes dont les plus grands crochets n'atteignent pas 40 μ.
B2 Longueur des bulbes de plus du tiers à environ la moitié de celle des bothridies.
B2b Plus grands crochets 20–24 μ. Gaines plus courtes que les bothridies.

Pars bulbosa en partie comprise dans *pars bothridialis*.

Velum court, plus court que chacune des autres parties du scolex, commencant assez loin an arrière des bulbes. *N. bisulcata* (E. Linton, 1889)."
The metacestodes from *L. pealeii* conform to the diagnosis of *N. bisulcata*.

Linton (1889a) described and figured tetrarhynchid cestodes from the dusky shark, *Carcharinus obscurus*, as a new species, *Rhyncobothrius bisulcatum*. He (1897a, p. 810) transferred the species to the genus *Tetrarhynchus*. In his report on larval cestode parasites of fishes, Linton (1897a) described and figured encysted larvae, identified as *Tetrarhynchus bisulcatum*, from a variety of hosts, including *Paralichthys dentatus, Cynoscion regalis, Tetranarce occidentalis, Stenotomus chrysops*, and *Seriola zonata*. The cysts were located principally in the mucous and submucous layers of the stomach. He noted, p. 810, "I have found it very abundant in the squeteague at Woods Hole, Massachusetts, and have seldom examined one of these fish without finding numerous examples of encysted tetrarhynchs in the stomach walls." The description and figures of these larvae (Pl. VI, Figs. 11–15) are so similar to the metacestodes from *L. pealeii* that their identity is apparent. Linton observed, p. 787, "The finding of a larval cestode parasite encysted in the tissues of a fish is not always proof that the fish is a true intermediate host. Beneden invented the term *xenosite* i.e., stranger-for this condition." Baer (1951, p. 12) designated such hosts as "hôtes d'attente" or paratenic hosts. Referring to *T. bisulcatus*, Linton (1897b) reported, p. 452, "I have found this species in the adult condition, thus far, only in the dusky shark (*Carcharhinus obscurus*)."

Linton (1924) reviewed his studies on the cestode parasites of sharks and skates. Discussing the species, *Tetrarhynchus bisulcatus* (Linton), he reported adult worms from *Carcharhinus obscurus* and *Carcharhinus milberti* with single specimens from the stomach of *Galeocerdo arcticus* and *Squalus acanthias*. Encysted larval stages were recorded from 18 species of fishes. As noted earlier, Dollfus (1929) transferred the species, *T. sulcatus* to *Nybelinia*. The finding of encysted metacestodes in both cephalopods and teleost fishes shows that these are merely paratenic hosts that acquired the parasites by ingestion of previous hosts and that the worms become mature only in the intestine of selachian fishes. The

FIGURES 11–16. Larval stages of marine metacestodes. The specimens depicted in these figures are deposited in the platyhelminth collection of the American Museum of Natural History under the assigned numbers. Figure 11: *Nybelinia bisulcata* (Linton, 1889) *provis.*, specimen 3.80 mm long (No. 898). Figure 12: section of a tentacle of specimen No. 898. Figure 13: *Nybelinia yamagutii* Dollfus, 1950, *provis.*, specimen 5.00 mm long (No. 899). Figure 14: section of tentacle of specimen No. 901. Figure 15: *Lacistorhynchus tenue* (van Beneden, 1958) *provis.*, specimen 1.52 long (No. 900). Figure 16: *Otobothrium crenacolle* Linton, 1890, *provis.*, specimen 1.40 mm long (No. 901).

fact that the final hosts are large, oceanic fishes explains the wide dispersal of the parasite.

SPECIES NUMBER VI. *Nybelinia yamagutii* Dollfus, 1960, *provis.* Figures 13, 14.

Five plerocerci of this species were removed from cysts in the wall of the stomach. The worms are similar in size and form, ovate, rounded to slightly flattened anteriorly, tapering posteriorly. They measure 4.3 to 5.0 mm in length and 1.90 to 2.30 mm in width. Greatest width is at the level of the bothridia, which are sessile with attached edges. The *pars bothridialis* is 1.75 to 2.00 mm long, the *pars postbothridialis* is 2.10 to 2.70 mm long. The *pars bulbosa* is about two-thirds as long as the *pars bothridialis*. It is distinctly posterior to the *pars bothridialis* and extends to the appendix. The appendix is 0.20 to 0.50 mm long; the velum is 0.20 to 0.30 mm long. The tentacular bulbs are 1.45 to 1.55 mm long and 0.22 to 0.28 mm wide. They are cylindrical, slightly attenuated at the ends and extend from the appendix about four-fifths of the distance to the *pars bothridialis*. The tentacle-sheaths are longer than the bulbs and shorter than the tentacles, which when fully extended may be 2.30 mm long. The tentacles, without hooks, are about 0.12 mm wide and there are about 50 rows of hooks. The hooks near the base of the tentacle are smaller with a special arrangement, and they increase in size toward the tip. One side of the tentacle bears small hooks, the other side bears large hooks (Fig. 14). The small hooks have oval bases, about 0.020 by 0.012 mm and are 0.030 to 0.035 mm long. The large hooks have longer and broader bases and measure 0.080 to 0.085 mm in length. The hooks stain intensely with the Semichon technique. The hook pattern is almost identical with that in the species described by Dollfus (1960) as *Nybelinia yamagutii*. It was based on postlarvae from the general cavity of *Liosaccus cutaneus* (Günther), a teleost taken off the coast of Dakar, West Africa. The description and figure by Dollfus show the tentacular bulbs extending to the bothridia, but the wall of the *postbothridialis* is crenate, which indicates retraction of the region with forward protrusion of the bulbs. The name *N. yamagutii* was selected because Yamaguti (1934) had described a similar species, *N. pintneri*, from the blue shark, *Prionace glauca*, taken on the Pacific coast of Japan.

In Species No. VI, the tegument contains fine, flattened spines; the edges of the bothridia bear longitudinal rows of long, closely set, cylindrical bristles; and the parenchyma is filled with secretory cells. In these respects it agrees with Species No. V, but they differ in the relative length of the postbothridial region, in the attached edges of the bothridia, in the location and length of the tentacular bulbs, and in the armature of the tentacles.

SPECIES NUMBER VII. *Lacistorhynchus tenue* (van Beneden, 1858) Pintner, 1913, *provis.* Figure 15.

Three specimens were recovered from the washings after dissection of the stomachs and caeca of squids. They are identified as plerocerci of *Lacistorhynchus tenue* (van Beneden, 1858), the only recognized species in the genus. Pintner (1913) erected the genus *Lakistorhynchus* with *Tetrarhynchus tenuis* P. J. van Beneden, 1858 as the type species. He listed the species *T. benedenii* Créty, 1890

and *T. gracile* Diesing, 1863, as synonyms. The species, *T. benedenii* was included originally in *Dibothriorhynchus* Diesing, 1850, and was transferred to *Tetrarhynchus* by Vaullegeard (1899). The species, *tenuis*, was renamed, *gracile*, and included in *Rhynchobothrius* Rudolphi, 1819 by Diesing (1863). Subsequent authors have consistently written the name *Lacistorhynchus tenuis* (van Beneden, 1858) Pintner, 1913. But Yamaguti (1959) determined that the Greek word, *rhynchos*, is a neuter noun and he adopted the spelling, *tenue*, for the name of the species.

The specimens had emerged from their cysts, but the blastocysts are intact and the plerocerci agree in all respects with the figure of this stage given by Dollfus (1942, Fig. 241, g). In all of them the scolex is retracted, bent in an inverted U-shape, and occupies from one-third to two-fifths of the total length. They are slightly smaller than the specimens described by Dollfus, who reported that the plerocerci become smaller as they mature and the definite structures are formed. The present specimens are 1.5 to 1.80 mm in length and 0.50 to 0.55 mm in width. There are two bothridia, notched posteriorly, 0.23 to 0.25 mm long and 0.15 to 0.17 mm wide. The tentacular bulbs are 0.15 to 0.18 mm long and 0.05 to 0.06 mm in diameter. The postbulbar appendix is 0.10 to 0.12 mm in length. The distance from the tentacular bulbs to the bothridia is 0.45 to 0.55 mm. The tentacular sheaths are coiled and since the tentacles are retracted, the armature can not be determined in detail. The hooks are apparently arranged in a chainette and extend almost all the way to the bulbs. The tegument bears fine spines and the blastocyst measures 0.80 to 0.90 mm in length and 0.35 to 0.40 mm in width.

These metacestodes have long been known. According to Dollfus (1942, p. 321), "La larve de ce tétrarhynque—en raison de la forme particulière qu'affecte généralement son kyste, comme aussi en raison de sa grande fréquence (étant rencontrée souvent par dizaines et même par centaines) dans les poissons comestibles les plus communs de nos marchés—a, depuis longtemps, attiré l'attention des helminthologistes." They were described by Deslongchamps (1824), and the strobilate stage of the species was described by van Beneden (1850) from *Galeus canis* taken at Ostende. Van Beneden (1870) predicated the identity of the two stages. The most complete account of the morphology, life-cycles, and taxonomy of these cestodes is contained in the monograph by Dollfus (1942).

Linton (1889a) described *Tetrarhynchus tenuicolle* Rudolphi, 1819 from *Mustelus canis* at Woods Hole, Massachusetts. He (1889b) decided that the species he had identified as *T. tenuicolle* was actually a new species, which he described as *Rhynchobothrium bulbifer*. The next year, (1890) he described a second species, *Rhynchobothrium heterospine*, which differed from *R. bulbifer* in the absence of a bulb behind the scolex. Linton (1924) reported adult stages of *R. bulbifer* from *Galeorhinus laevis, Squalus acanthias,* and *Vulpecula marina*. He noted, p. 58, "The cysts and plerocerci of this species are often club-shaped, or gourd-shaped, the larger end being subglobular, the remainder, which is of much smaller diameter and cylindrical, may be either straight or curved. Usually encysted on viscera, and in intestinal wall, but common in the flesh of sand eels, silverside, and young herring." The cysts were recorded from 35 species of fishes in the period 1895–1924. The larval stage of *R. heterospine* was reported from four species of fish. Vaullegeard (1899) announced the identity of *R. bulbifer* and *R. tenuis* van Beneden, 1858. Pintner (1913) noted the similarity between *R. hetero-*

spine Linton, 1890 and *R. tenuis*, and Dollfus (1942) after examination of many larval and adult specimens declared the identity of the three species, *R. tenuis*, *R. bulbifer*, and *R. heterospine*.

SPECIES NUMBER VIII. *Otobothrium crenacolle* Linton, 1890, *provis.* Figure 16.

Two small metacestodes, found in the washings of dissections of stomach and caeca of squids are referred to this species. The specimens measure 1.2 and 1.4 mm in length; 0.5 and 0.56 mm in greatest width. They are rounded anteriorly and widest at the level of the posterior ends of the bothridia. The bothridia are patelliform, longer than wide, convergent anteriorly and divergent posteriorly, with deep median incisions and free ends. They are 0.60 to 0.67 mm long and have thickened edges that bear longitudinal rows of closely-set, long, cilia-like bristles. Lightly staining circular areas near the posterior ends of the bothridial lobes probably represent the described eversible, ciliated pits. The tegument contains very small flattened spines. The tentacular bulbs are oval, 0.12 to 0.15 mm long and 0.036 to 0.042 mm wide. They are situated at the posterior end of the scolex and do not extend forward to the level of the bothridia. The tentacular sheaths are longer than the tentacles, which are almost completely retracted and in this condition measure 0.26 to 0.29 mm long and 0.012 to 0.015 mm wide. The armature is heteracanth, with alternate rows of large and small hooks but only the spines at the anterior ends of the sheaths are clearly visible and the pattern is indistinct. The large hooks are curved with firm bases, 10 to 12 μ long; the small hooks are 3 to 4 μ long. The velum is 0.15 to 0.22 mm long; the appendix is 0.24 to 0.35 mm long and 0.26 to 0.30 mm wide. The shape and size of the tentacular bulbs distinguish these specimens as *O. crenacolle*.

Dollfus (1942) erected a new family, *Otobothriidae* to contain *Otobothrium* Linton, 1890 and *Poecilancistrium* Dollfus, 1929. He gave a more precise generic diagnosis of *Otobothrium* and proposed a new subgenus, *Pseudotobothrium*, to receive *Otobothrium dipsacum* Linton, 1897. Discussing the genus he predicated, p. 239, "Il y a quelques espèces encore très mal connues, qui ne peuvent pas être classées avc certitude dans un des deux sous-genres. Parmi les dix espèces admises ici dans le genre *Otobothrium*, il y en a vraisemblablement de synonymes; les descriptions publiées sont incomplètes et beaucoup de figures sont insuffisantes, surtout en ce qui concrne l'armature des trompes." These worms are parasites of wide-ranging oceanic fishes, and Linton, (1934) commenting on the distribution of helminth Entozoa of fishes of the Woods Hole region (Massachusetts, U.S.A.), stated, p. 130, "While the adult stages of selachian cestodes are limited to one or a few hosts, the encysted stage appears to be tolerated in any fish in which it may obtained lodgement. Thus, the species *Otobothrium crenacolle* Linton, has been found in cysts, usually on the viscera or in the submucosa of the stomach or intestine, of 16 species of fish, including four species of shark, and *Otobothrium imparispine* Linton has been recorded from 37 species of teleosts."

SUMMARY

Metacestoid stages of tetraphyllidean and tetrarhynchidean cestodes were described from marine fishes by O. F. Mueller (1787), Fabricius (1794), and

Cuvier (1817). Although known for more than a century, knowledge of these tapeworms is meager, and the life-cycle has not been experimentally demonstrated for any one of them. The worms mature only in the spiral valve of elasmobranch fishes, but larval and developmental stages occur in a great variety of marine invertebrates as well as in fishes. Technical difficulties of maintaining experimental hosts for long periods under controlled laboratory conditions have precluded the successful completion of life-histories. After a period of incubation, the eggs contain motile larvae, oncospheres, which, when eaten by copepods, migrate to the body cavity and transform into second stage larvae, procercoids. When the copepods are eaten, the procercoids emerge from the intestine of the second intermediate host and enter the body cavity or penetrate adjacent tissues where they develop into plerocercoids and may be encapsulated. If the second intermediate host is eaten by other than an elasmobranch, the plerocercoids may again emerge from the intestine and be re-encysted. Thus, a plerocercoid may pass through a series of intermediate hosts before arriving at a suitable selachian host. Such residence in successive paratenic hosts provides for long life for the individual and wide distribution and dispersal of the species. The life-cycle, accordingly, is essentially a food chain, with a shark, skate, or ray serving as the final link.

Data compiled from literature encompasses the biology and bionomics of these cestodes, their development, intermediate and definitive hosts, taxonomy and nomenclature. Descriptions are presented of eight species of metacestodes from squids taken in the Cape Cod area. They are provisionally assigned to species, four in the order Tetraphyllidea and four in the order Tetrahynchidea.

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